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SPECIAL PAPER

THE ORIGIN OF COASTAL SAGE VEGETATION, ALTA AND BAJA CALIFORNIA[1]

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ABSTRACT

Coastal sage is a new pioneer-type vegetation that only spread widely after the Early Quaternary, when species on the dry open borders of forest, woodland and arid tropic scrub vegetation shifted into expanding dry sites there and in adjacent grasslands. These new sites were created by a coincidence of major climatic and tectonic events and by accompanying erosion and mass movement on steep new slopes. Attaining most of its present area during the hot, dry Xerothermic, coastal sage scrub spread further as man's activities disturbed the landscape.

WE KNOW relatively little about the coastal sage vegetation of cismontane California and adjacent Baja California which is rapidly disappearing under spreading urbanization. Lists of species that contribute to coastal sage scrub, the ecologic relations of some of the taxa, and the general nature of its communities are presented in recent analyses (e.g., Thorne, 1976; Mooney, 1977; Heady et al., 1977; Kirkpatrick and Hutchinson, 1977). These and most previous articles provide little or no information with respect to the age and origin of the vegetation itself: how and when did it originate? A notable contribution to this problem is the analysis by Epling and Lewis (1942) of the distribution and floristic relations of coastal sage taxa. They show that greatest diversity is in the Diegan area (San Diego region southward into coastal Baja California) and that many of the taxa appear to have been derived from "Miocene vegetation which entered the southwestern United States from the north Mexican plateau (p. 462)." This appears to be true for many of the Diegan taxa. However, to the north in coastal California increasing numbers of taxa in coastal sage vegetation have affinities with alliances that link them with temperate forests.

That coastal sage taxa have come from other vegetation zones, and have adapted to new conditions, was suggested also by Shreve (1936) in discussing vegetation in the transition (Diegan sage as used here) from Sonoran Desert to chaparral. As he notes, chaparral species extend southward into the transition (Diegan sage) to desert as long as there is adequate moisture, but the northern distribution of Sonoran Desert taxa into Diegan sage depends on other (unspecified) factors. The most important one, apart from an absence of frost, appears to be adequate summer moisture, even though it is small in amount (see Raven and Axelrod, 1978, p. 55). Epling and Lewis (1942) in discussing the source of *Fraxinus trifoliata* and *Satureja chandleri*, and Raven and Mathias (1960) in considering the origin and history of *Sanicula deserticola*, point out that these coastal sage species probably were derived from ancestral taxa represented now by allied species in chaparral vegetation.

Of these species, *Fraxinus trifoliata* is certainly an ancient taxon for it occurs in essentially modern form in the Miocene. Other distinctive taxa in Diegan sage that also have had a long history, as judged from their occurrence as similar species in the Miocene and Pliocene, are *Aesculus palmeri*, *Baccharis sergiloides*, *Malosma laurina* and *Rhus integrifolia*. Although they are typical of coastal sage today, and enter chaparral only marginally in disturbed areas, their present restriction to coastal sage vegetation need not mean that this vegetation has great age, contrary to the dicta of some paleoecologists. In this respect, it is recalled that chaparral is not an ancient zonal vegetation. Evergreen sclerophylls no doubt formed restricted seral communities in local dry sites as far back as the later Eocene. However, during most of the Tertiary, sclerophyllous shrubs contributed chiefly to the understory of a rich live oak-laurel-madrone woodland (Axelrod, 1975).

Commencing in the Late Miocene, all plants in the region were subjected to a trend to pro-

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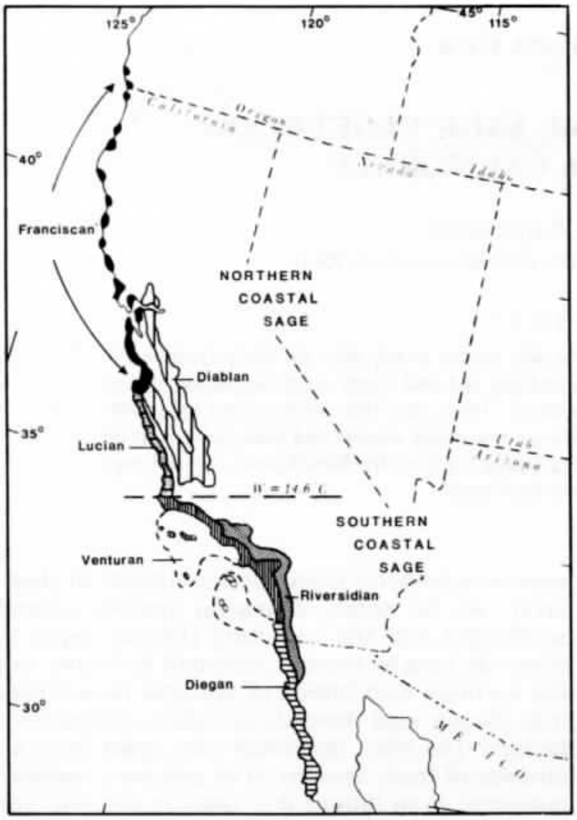

Fig. 1. General areas occupied by the major divisions of coastal sage vegetation. Areas greatly exaggerated owing to large map scale.

gressively drier climate, to the elimination of summer rain and, since the Early Pleistocene, to the emergence of a progressively more severe mediterranean climate of dry summers. In addition, plants have responded to new habitats created by major mountain building during the Quaternary. Available evidence suggests that chaparral originated as a zonal type of vegetation during the middle and later Quaternary in response to these factors (Axelrod, 1975). The present thesis is that coastal sage is also a new regional type of vegetation that developed under the impetus of these same factors, but in a belt of drier climate at elevations below chaparral. To understand how and when it originated, some of the salient features of living coastal sage scrub are reviewed first.

GENERAL NATURE—*Area*—Coastal sage is scattered along the coast from Oregon into Baja California, reaching into the inner Coast Ranges of central California and the Transverse and Peninsular Ranges of southern California and Baja California. It regularly inhabits the driest sites, notably steep south slopes with thin soil, rocky areas, exposed sea bluffs, coastal and river terraces composed of coarse alluvial outwash, and coastal dunes. Coastal sage has a generally patchy distribution in the north and also in the south, though its area gradually widens there as aridity increases. The general region it occupies is indicated only in a general way in Fig. 1 because the acreage it occupies over much of the region is so limited that it cannot be depicted at this scale. The typical spotty distribution and small areas it covers are shown on the vegetation-type maps made by the California (now Pacific Southwest) Forest and Range Experiment Station during the 1930's. Mooney (1977, Fig. 13-3) presents a copy of one of them that illustrates its occurrence in the Pt. Dume area, southern California.

Physiognomy—The homogeneity of coastal sage vegetation results from the soft-stemmed nature of its shrubby dominants. Typically non-sclerophyllous—the "soft chaparral" of Jepson (1925)—they are relatively low in stature, mostly from 0.5 to 1.5 meters in height. They contribute to a vegetation that is not as dense or as rigidly branched as chaparral and is therefore relatively easy to penetrate. Although a few sclerophyllous taxa occur in the community they do not dominate coastal sage as the hard-leaved taxa that characterize chaparral which regularly lies above it in areas of higher rainfall.

The life forms of coastal sage taxa change gradually from north to south. In the north, evergreen shrubs (*Arctostaphylos*—very rare, *Garrya*, *Gaultheria*, *Ledum*—wet sites, *Vaccinium*) from the bordering forests as well as winter-deciduous (*Dirca*—very rare, *Holodiscus*, *Ribes*, *Rubus*, *Toxicodendron*) and drought-deciduous (*Ambrosia*, *Artemisia*, *Baccharis*, *Lupinus*) shrubs make up the vegetation. To the south, drought-deciduous taxa (*Ambrosia*, *Artemisia*, *Baccharis*, *Lupinus*) make up the vegetation. To the south, drought-deciduous taxa (*Ambrosia*, *Artemisia*, *Baccharis*, *Encelia*, *Haplopappus*, *Salvia*, *Viguiera*) increase in importance, and different evergreens (*Cneoridium*, *Malosma*, *Rhus*) occur in the coastal strip. In addition, in coastal areas from near the Mexican border southward, and also on the Catalinan islands, stem succulents (e.g., *Agave*, *Bergerocactus*, *Dudleya*, *Euphorbia*, *Mammillaria*, *Opuntia*) rapidly become a regular part of the vegetation which reaches southward to the vicinity of El Rosario, Baja California, where it is replaced by Sonoran Desert vegetation. The gradual shift in the adaptive nature of the dominants results from their utilization of moisture in the upper part of the soil in the moist, cool part of the year. As progressively drier climate appears to the south,

TABLE 1. *Comparison of some classifications of coastal sage vegetation*

Munz and Keck (1949)	Heady and others (1977); Mooney (1977)	Thorne (1976)	Kirkpatrick and Hutchinson (1977)	Axelrod (1950), and this report
Northern coastal scrub	Northern coastal scrub	Northern coastal scrub	Northern coastal scrub	Northern coastal sage Franciscan sage Lucian sage Diablan sage
Coastal sage scrub	Southern coastal scrub	Southern coastal sage scrub	Southern coastal scrub	Southern coastal sage
	Coastal sage scrub	a. Sea-bluff succulent b. Maritime sage scrub c. Inland sage scrub	. . . Venturan sage . . . . Riversidian sage	Venturan sage Riversidian sage
	Succulent scrub	Maritime desert scrub	San Diegan sage	Diegan sage

the taxa avoid the longer period of summer drought by shedding their leaves, or by storing water in their stems (Mooney et al., 1970; Mooney and Harrison, 1972; Mooney, 1977).

Ecologic occurrence—Over much of its area coastal sage occupies sites that recently were grassland. This is evident in the region from Del Norte and Mendocino counties southward into Monterey County, areas where grassland ("coastal prairie") adjacent to conifer forest and mixed evergreen forest has patches of sage. The relation is seen also in the central Coast Ranges, where coastal sage has a patchy distribution in grassland and alternates on slopes with patches of live oak woodland-grass, digger pine-oak woodland-grass, closed-cone pine forest, or chaparral. Similarly, in southern California coastal sage regularly occurs in grassland adjacent to oak woodland-grass or walnut woodland-grass and at levels below chaparral where rainfall is lower. Even in areas where it appears to be "climax" vegetation, as on the coast south of Monterey, in central Ventura County east of Ojai, or in northern Baja California, coastal sage covers slopes in terrains where relict patches of grassland are confined to relatively deep soils on the crests of the ridges and spurs. Such occurrences are well documented on the original vegetation maps of the California Forest and Range Experiment Station made in the 1930's.

There are important exceptions to the frequent occurrence of coastal sage scrub in grassland areas. It also inhabits terrains that are largely covered with woodland, or woodland-grass, or forest. There it is confined to the driest sites, as steep south slopes, areas with thin or little (or no) soil, or especially well-drained sandy or gravelly substrates (dunes, river terraces, marine terraces). From San Diego County southward into Baja California coastal sage dominates two major terrains—broad coastal terraces and steep slopes carved into the granitic-metamorphic basement rocks. The coastal terraces, composed of coarse conglomerate or conglomeratic sandstone, provide a substrate too dry for a grassy turf, as do the steep slopes in basement rocks. There is little or no soil to support a turf of grass because the area has been repeatedly burned and stripped of soil by erosion, and overgrazing has resulted in further severe erosion. Even within this highly disturbed landscape relict patches of grassland still occur in local areas, as near San Vicente and in the mountains east of Santo Tomas. In addition, along the highway south of Manadero relict *Quercus agrifolia* woodland-grass vegetation implies that wider grasslands were there prior to clearing and cultivation. Finally, there is one other, more localized occurrence for coastal sage. This is in stabilized dune terrains scattered along the coast, as in the hills south of Morro Bay, on the Lompoc plain, the Santa Maria plain, and elsewhere as discussed by Barbour and Johnson (1977). Dune sage vegetation grades seaward to coastal-bluff sage or to beach vegetation and many species are common to them. Dune sage scrub is therefore no more than the seaward or maritime edge of coastal sage scrub, changing composition southward along the coastal strip with it.

Communities—Coastal sage vegetation is represented by several major associations (Table 1). I prefer the geographic (regional) designation because the name calls to mind the area and nature of the environment in which each lives, and avoids the confusion that now exists in the similarity of terminology that has been proposed. The major types cannot be designated by species that distinguish them because each one has several communities that differ in composition depending on exposure, soil depth, successional relations, and local climate. The diverse communities are shown on the vegetation maps made

TABLE 2. *Shrubs contributing to the several divisions of coastal sage scrub; forbs and grasses not listed. XX = common and important; X = present to rare; 0 = absent, or very rare*

	Franciscan	Lucian	Diablan	Riversidian	Venturan	Diegan
Conifer forest						
Corylus californica	XX	X	0	0	0	0
Pteridium aquilinum	XX	0	0	0	0	0
Ribes sanguineum	XX	0	0	0	0	0
Rubus vitifolius	XX	0	0	0	0	0
Symphoricarpos albus	XX	0	0	0	0	0
Toxicodendron diversilobum	XX	0	X	0	X	0
Closed-cone pine forest						
Arctostaphylos andersonii	X	X	0	0	0	0
Arctostaphylos crustacea	X	X	0	0	0	0
Arctostaphylos edmundsii	0	X	0	0	0	0
Arctostaphylos hookeri	0	X	0	0	0	0
Arctostaphylos pumila	0	X	0	0	0	0
Arctostaphylos rudis	0	X	0	0	0	0
Ceanothus gloriosus	X	0	0	0	0	0
Ceanothus griseus	X	X	0	0	0	0
Ceanothus maritimus	0	X	0	0	0	0
Ceanothus ramulosus	X	X	0	0	0	0
Ceanothus rigidus	0	X	0	0	0	0
Ceanothus thyrsiflorus	X	X	0	0	0	0
(*Note:* above taxa scattered in a matrix of coastal sage)						
Galvesia speciosa	0	0	0	0	X	XX
Gaultheria shallon	XX	X	0	0	0	0
Myrica californica	XX	X	0	0	X	0
Vaccinium ovatum	XX	X	0	0	0	0
Woodland-chaparral						
Aesculus parryi	0	0	0	0	0	X
Artemisia californica	XX	XX	XX	XX	XX	0
Coreopsis gigantea	0	X [S. edge]	0	0	XX	X
Coreopsis maritima	0	0	0	0	0	X
Diplacus aurantiacus	XX	XX	X	X	XX	0
Eriogonum fasciculatum	0	0	0	0	XX	X
Eriogonum fascic. v. *foliolosum*	0	XX	XX	XX	XX	X
Eriogonum fascic. v. *poliofolium*	0	0	X	XX	0	0
Eriogonum giganteum	0	0	0	0	0	X
Eriogonum latifolium	XX	XX	0	0	0	0
Eriophyllum confertifolium	XX	XX	XX	0	XX	0
Eriophyllum stachaedifolium	XX	X	0	0	0	0
Eriophyllum nevinii	0	0	0	0	XX	XX
Eriodictyon crassifolium	0	0	0	XX	0	0
Fraxinum trifoliata	0	0	0	0	0	XX
Haplopappus (Stenotopsis) linearifolius	0	0	XX	XX	0	0
Haplopappus (Hazardia) squarrosus	0	XX	XX	0	XX	0
Haplopappus (Isocoma) venetus	X	X	XX	0	XX	XX
Helianthemum scoparium	0	0	0	0	XX	0
Lavatera assurgentifolia	0	0	0	0	XX	XX
Lotus scoparius	0	X	X	XX	X	XX
Lupinus albifrons	X	XX	XX	0	0	0
Lupinus arboreus	XX	XX	0	0	X	0
Lupinus chamissonis	XX	XX	0	0	X	0
Malacothamnus fasciculatus	0	0	0	XX	0	XX
Malosma laurina	0	0	0	0	XX	XX
Ptelea aptera	0	0	0	0	0	X
Rhamnus californica	XX	XX	0	0	XX	0
Rhamnus crocea	0	XX	0	0	XX	0
Rhamnus insulus	0	0	0	0	XX	XX
Rhus (Schmaltzia) integrifolia	0	0	0	0	XX	XX
Ribes tortosum	0	0	0	0	0	XX
Rosa minutifolia	0	0	0	0	0	XX
Salvia apiana	0	0	0	XX	XX	X

TABLE 2. *Continued*

	Franciscan	Lucian	Diablan	Riversidian	Venturan	Diegan
Salvia leucophylla	0	0	0	XX	XX	X
Salvia mellifera	0	XX	XX	XX	XX	0
Salvia munzii	0	0	0	0	0	XX
Venegasia carpesioides	X	XX	0	0	XX	X
Arid tropic scrub/semidesert						
Acalypha californica	0	0	0	0	0	XX
Agave shawii	0	0	0	0	0	XX
Agave goldmannii	0	0	0	0	0	XX
Ambrosia (Franseria) ambrosioides	0	0	0	0	0	XX
Ambrosia (Franseria) chamissonis	XX	XX	0	0	XX	X
Ambrosia (Franseria) chenopodiifolia	0	0	0	0	0	XX
Artemisia californica	XX	XX	XX	XX	XX	X
Atriplex californica	XX	XX	0	0	XX	X
Atriplex canescens	0	0	XX	XX	XX	X
Atriplex lentiformis v. *breweri*	X	X	0	0	X	0
Atriplex polycarpa	0	0	XX	0	0	0
Baccharis pilularis	XX	XX	XX	XX	XX	X
Bergerocactus emoryi	0	0	0	0	0	XX
Capparis (Isomeris) arboreus	0	0	X	XX	X	X
Chrysothamnus nauseosus v. *mohavensis*	0	0	XX	0	0	0
Cneoridium dumosum	0	0	0	0	X	XX
Dudleya spp.	0	0	0	0	X	XX
Echinocereus maritimus	0	0	0	0	X	XX
Encelia californica	0	0	XX	XX	XX	XX
Encelia farinosa	0	0	0	XX	0	0
Ephedra californica	0	0	0	0	0	XX
Euphorbia misera	0	0	0	0	X	XX
Gutierrezia californica	0	0	XX	XX	0	0
Haplopappus (Ericameria) ericoides	XX	XX	0	0	XX	0
Haplopappus (Ericameria) pinifolius	0	0	0	XX	X	0
Lycium brevipes	0	0	0	0	0	XX
Lycium californicum	0	0	0	0	0	XX
Machaerocereus gummosus	0	0	0	0	0	XX
Mammillaria spp.	0	0	0	0	0	XX
Opuntia litoralis	0	0	0	0	X	XX
Opuntia spp.	0	0	0	X	X	XX
Simmondsia chinensis	0	0	0	0	0	XX
Stephanomeria pauciflora	0	0	0	X	0	0
Viguiera deltoidea v. *parishii*	0	0	0	0	0	XX
Viguiera laciniata	0	0	0	0	X	XX
Yucca whipplei	0	0	X	XX	XX	X

by the California (now Pacific Southwest) Forest and Range Experiment Station in the 1930's and were discussed recently for the Riversidian sage of interior southern California (Kirkpatrick and Hutchinson, 1977).

The species that contribute to coastal sage scrub occur also in other vegetation zones (Table 2). As listed there, some of the taxa contribute to two or more major sage communities, as shown by *Ambrosia (Franseria) chenopodiifolia*, *Artemisia californica*, *Baccharis pilularis*, *Encelia californica*, *Salvia mellifera* and others. As a result, the major divisions of coastal sage intergrade. Along the coastal strip, Franciscan sage passes into the Lucian, and the Diegan into the Venturan. The Lucian and Franciscan communities are replaced in the drier interior by an impoverished sage here termed Diablan for its development in the Diablo Range and in other inner Coast Ranges. Similarly, in southern California, Venturan and Diegan sage of the coastal strip give way in the interior to the impoverished Riversidian sage.

The floristic relationships of the divisions of coastal sage are summarized in Table 3. The percentage similarity between the groupings, as based solely on species presence or absence, is as follows: (1) the north coastal divisions, Franciscan and Lucian, are more similar to one another (81%) than either is to the south coastal divisions; (2) the south coastal divisions, Venturan and Diegan, are more similar to one another (61%) than either is to the north coastal divisions; (3) the interior divisions, Diablan and Riversidian, are more similar to one another (67%) than either is to any of the coastal divi-

TABLE 3. *Floristic relationships of the various divisions of coastal sage vegetation*[a]

	Franciscan (32 sp.)	Lucian (42 sp.)	Diablan (22 sp.)	Riversidian (23 sp.)	Venturan (44 sp.)	Diegan (51 sp.)
Franciscan	\	30	9	5	16	6
Lucian	81	\	13	8	22	9
Diablan	33	41	\	15	16	9
Riversidian	18	25	67	\	16	12
Venturan	42	51	48	48	\	29
Diegan	14	19	25	32	61	\

NUMBER OF TAXA IN COMMON (above diagonal)

PERCENT SIMILARITY (below diagonal)

[a] Percent similarity was calculated with the index of Sorensen (1948):

$$\% = \frac{2c}{a + b} \times 100$$

where a is the total number of taxa in division a, b is the total number of taxa in division b, and c is the number of taxa common to the divisions a and b.

TABLE 4. *Mean annual rainfall for divisions of coastal sage (data for stations in Fig. 2)*

	cm	in.
North coastal sage		
Franciscan	585	23
Lucian	405	16
Diablan	430	17
South coastal sage		
Venturan	380	15
Diegan	230	9
Riversidian	330	13

sions; and (4) Venturan sage shares approximately one-half of its species with each of the other divisions. This high degree of similarity of Venturan sage to the others probably reflects its central position geographically and climatically. In addition, its area was affected importantly during the Wisconsin by the southward migration of taxa from the coastal province to the north, and during the Xerothermic by the coastward migration of taxa from the interior.

Diegan sage has a larger number of unique taxa than the other divisions. Among these are *Acalypha californica, Agave shawii, Aesculus palmeri, Cneoridium dumosum, Euphorbia misera, Fraxinus trifoliata, Lycium californicum, Ptelea aptera, Ribes tortuosum, Rosa minutifolia, Simmondsia chinensis, Yucca schidigera*, and species of cacti distributed in *Bergerocactus, Echinocereus, Ferocactus, Machaerocereus, Myrtillocactus, Optunia*, and others. Many of them range southward into the Sonoran Desert (Shreve, 1936). Diegan sage also has a greater diversity of life forms than the other divisions of coastal sage. This probably reflects the warmer winter climate and more occasional summer rain as compared with areas of coastal sage to the north. In this regard, the chaparral of Coahuila and Nuevo Leon (Muller, 1939, 1947), as well as that of Arizona (personal observation), is also a more diversified community than that in California. These eastern associations have taxa that belong to genera that are not typical components of chaparral in California, notably species of *Agave, Amelanchier, Arbutus, Cowania, Juniperus, Mahonia, Nolina, Philadelphus, Pinus* (*cembroides*), as well as leguminous shrubs, notably *Acacia, Calliandra, Leucaena, Robinia* and *Sophora*. They range from chaparral into the adjacent, more mesic woodland and also into semiarid scrub and grassland at lower, drier levels. That this wider ecologic amplitude may be the result of summer rain seems likely. Significantly, a comparable mixture of chaparral taxa occurs today along the desert slopes of the Peninsular Ranges from near Banner (below Julian) southward, an area where summer rain occurs in greater frequency than on the coast or to the north (Raven and Axelrod, 1978, p. 56). The greater diversity of these communities in areas with summer rain recalls the nature of the richer vegetation zones that existed in the western United States during the Miocene and Pliocene. The taxa of these ancestral communities were segregated into new environments, to those with narrower climatic parameters (see Axelrod, 1976, 1977). This implies that the ancestral Neogene sage, which was highly restricted in area (see below), was also more diverse than its modern derivatives, an inference supported by the nature of the associates of fossil sage species as outlined below.

Climate—Yearly precipitation gradually decreases southward over the area occupied by coastal sage, and it also decreases to the east, in the lee of the Coast Ranges. In the north, precipitation comes in the cooler half of the year and temperatures are relatively mild. To the south, as temperature rises and rainfall decreases, effective moisture is lower and coastal sage vegetation shows a progressive change in response to it. Near the Mexican border, summer rain increases in frequency and adds an important (though small) amount to the yearly total,

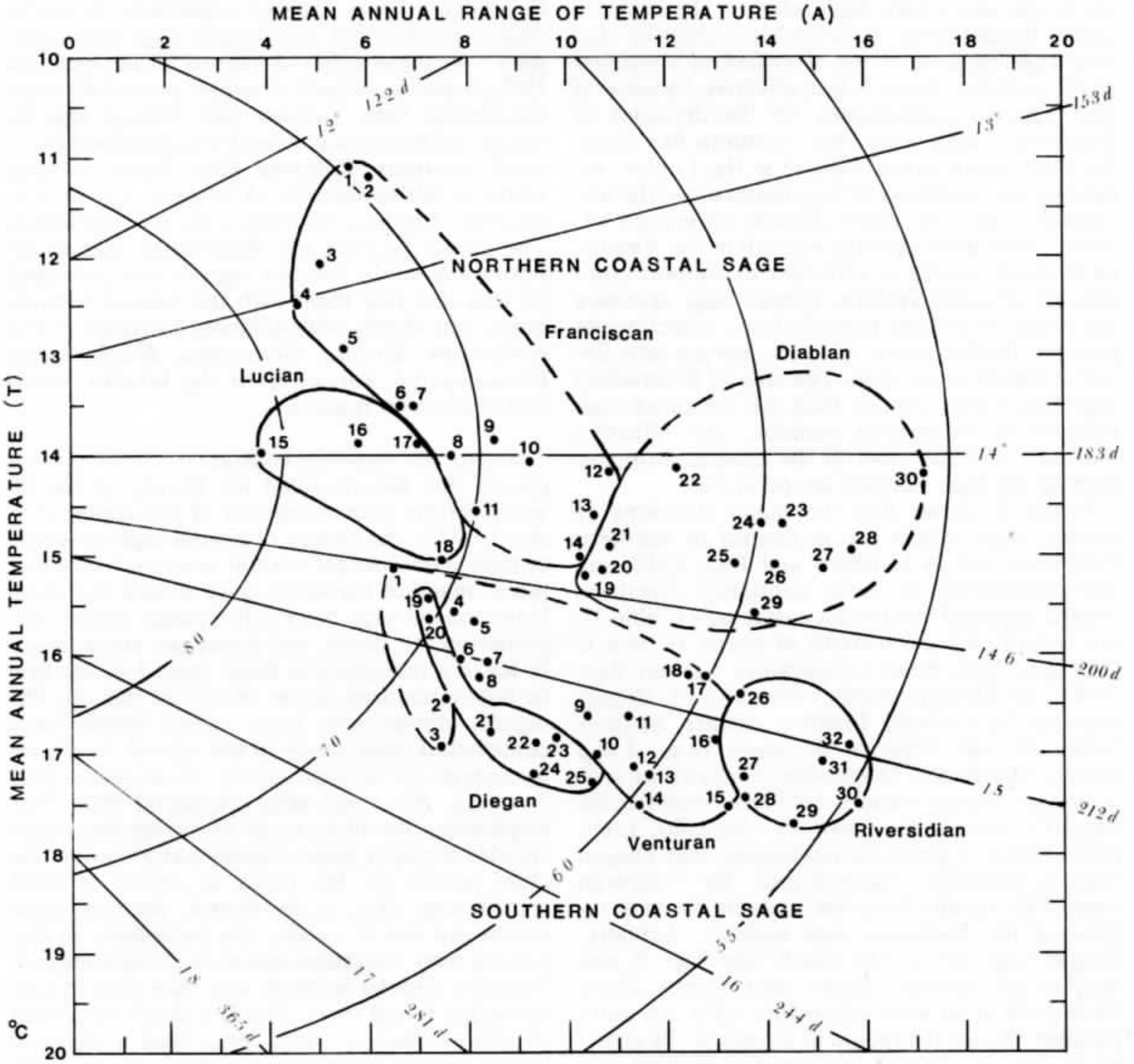

Fig. 2. Comparison of thermal parameters of Northern coastal (Franciscan, Lucian, Diablan) and Southern coastal sage (Venturan, Riversidian, Diegan). Radians are lines of Warmth *(W)* designating the number of days *(d)* with mean temperature greater than *W*°C, arcs indicate equability (M) rating (see Bailey 1960; 1964).

NORTHERN COASTAL SAGE—*Franciscan*. 1—Ft. Bragg, 2—Eureka, 3—Pt. Arena, 4—Ft. Ross, 5—Pt. Arguello, 6—Watsonville, 7—Monterey, 8—Salinas, 9—SF A/P, 10—Oakland A/P, 11—Richmond, 12—Petaluma, 13—Napa, 14—San Rafael. *Lucian*. 15—Morro Bay, 16—Lompoc, 17—Santa Maria, 18—San Luis Obispo. *Diablan*. 19—Hollister, 20—San Jose, 21—King City, 22—Sonoma, 23—Paso Robles, 24—Walnut Creek, 25—Martinez, 26—Livermore, 27—Pinnacles N. M., 28—Mt. Diablo N. Gate, 29—Fairfield, 30—Cyuama.

SOUTHERN COASTAL SAGE—*Venturan*. 1—Oxnard, 2—San Pedro, 3—UCLA, 4—Oceanside, 5—Santa Barbara, 6—Newport Beach, 7—Laguna Beach, 8—Santa Paula, 9—Tustin, 10—Santa Ana, 11—Escondido, 12—Pasadena, 13—San Fernando, 14—San Gabriel, 15—Sunland, 16—Claremont, 17—Ojai, 18—Upland. *Diegan*. 19—La Mission, 20—Avalon, 21—Ensenada, 22—Tijuana, 23—El Rosario, 24—San Diego, 25—San Vicente. *Riversidian*. 26—Ramona, 27—Riverside, 28—Santo Tomas, 29—San Bernardino, 30—Elsinore, 31—Redlands, 32—San Jacinto.

and at an especially critical time of the year (Raven and Axelrod, 1978, p. 55–59).

Table 4 lists the average annual precipitation for all stations representing each division of coastal sage presented in Fig. 2. Total rainfall is higher in the northern than the southern sector, and is highest in the Franciscan sage which borders forest for the most part. The lower rainfall for Lucian sage reflects its more southerly position and also the low elevation of the stations along the coastal strip; rainfall in the Santa Lucia Range is much higher than the average listed ow-

ing to the abnormally high relief on the seaward slope. Precipitation is somewhat higher for Diablan sage because of the elevation of a number of the stations, but it is less effective because of high summer temperature. Of the divisions of Southern coastal sage, the Venturan has about the same mean annual rainfall as the Lucian, reflecting the continuity of vegetation along the low coastal strip. The chief climatic difference between them is the greater warmth in the Venturan division, which is sufficient to support commercial avocado culture. Diegan sage occupies the areas of lowest precipitation, reflecting its position farther south where it merges into Sonoran Desert vegetation. The area of Riversidian sage has a drier climate than the Venturan sage because of its interior position, and effective moisture is lower than in the coastal strip, reflecting the high summer temperature.

Figure 2 shows that the major divisions of coastal sage, which are in central to northern California and in southern and Baja California and correspond to those captioned Northern coastal sage and Southern coastal sage (Table 1), are separated by a warmth of about *W* 14.6 C (200 days with mean temperature warmer than 14.6 C; or 200 days warmer than 58.3 F). Diegan sage lies in a wholly frostless climate, as does Venturan sage close to the coast (e.g., Long Beach, San Pedro, Oceanside, Oxnard), as well as certain coastal stations for Franciscan-Lucian sage (Pt. Arena, Ft. Ross, Pt. Arguello, Lompoc). Figure 2 gives the impression that Diegan sage is partially "surrounded" by Venturan sage. This results from the equable thermal regime of the Venturan sage stations. Actually, Diegan sage lies to the south (see Fig. 1) and reaches its northern limits near Torrey Pines State Park in an area where July rains are more frequent than in the region to the north. As charted in Fig. 2, climatic stations for Diablan and Riversidian sage in the interior have higher ranges of temperature and hence a climate less equable than that of the coastal strip.

Summary—In northern to central California, there is a gradual transition southward from Franciscan to Lucian sage, the former including taxa derived from forest (*Corylus, Ribes, Rubus, Toxicodendron*) woodland-chaparral (*Diplacus, Eriophyllum, Lupinus*) and arid tropic scrub/semidesert (*Ambrosia, Atriplex, Baccharis, Eriogonum, Haplopappus*) vegetation, and with members of the latter increasing in importance southward. Lucian is replaced by the more diverse Venturan sage in coastal southern California where climate is warmer. Its taxa were derived from woodland (*Ericameria, Haplopappus, Helianthemum, Malosma, Rhus*) and arid tropic scrub/semidesert (*Coreopsis, Eriogonum, Encelia, Salvia, Lotus, Yucca*) vegetation. It grades southward into the rich Diegan sage that occupies a frostless area transitional to the Sonoran Desert, and is subject to winter as well as regular, though light, summer rain. Diegan sage includes ancient taxa derived from woodland (*Aesculus, Fraxinus, Malosma, Rhus, Ribes*) and arid tropic scrub/semidesert (*Acalypha, Agave, Euphorbia, Lycium, Machaerocereus*) vegetation. The poorer Diablan and Riversidian sage of the hotter and colder interior regions are composed of taxa that link them with the coastal communities, but chiefly with alliances [*Atriplex, Chrysothamnus, Encelia, Gutierrezia, Haplopappus* (*Stenotopsis*), *Yucca*] from the interior desert and semidesert regions.

Fossil record—In contrast to the rich fossil record that has revealed the history of the diverse forests and woodlands of the region (Axelrod, 1977), the history of coastal sage scrub has remained obscure for several reasons. In the first place, many of the semiwoody shrubs that dominate coastal sage have soft, spongy leaves that wither on the stems, and hence are not as likely to leave a recognizable fossil record as the firm or heavy textured leaves of elm or oak. In this regard, shrubs with hard, scleric leaves have contributed importantly to the record, as shown by species of *Arctostaphylos, Ceanothus, Heteromeles, Rhus* and other chaparral taxa. This emphasizes the importance of having structures suitable for easy preservation, and pinpoints the chief reason for the rarity of leaves of most coastal sage taxa in the record. Second, since shrubs are low in stature, the probability of dispersing their structures into an accumulating sedimentary deposit is much less than that of tall, spreading forest trees. Third, a shrub has fewer structures (leaves, seeds, etc.) than a tree and hence cannot contribute as much to an accumulating record. Fourth, coastal sage vegetation largely inhabits slopes so that entry of the remains of its taxa into pools of plant accumulation is not as likely as for the structures of trees that live on the borders of a lake or stream. And fifth, since coastal sage occurs chiefly in areas of relatively low 250–380 mm (10–15 inches), seasonally distributed (winter) rainfall, the sedimentary record is not accumulating as widely and as continuously as in regions where precipitation is sufficient to support forests and woodlands of regional extent.

Nonetheless, some of the woody shrubs that contribute to coastal sage vegetation in central to northern California (e.g., *Baccharis pilularis, Garrya elliptica, Ribes sanguineum, Symphoricarpos albus, Toxicodendron diversilobum*) and in southern and Baja California (e.g., *Aesculus palmeri, Baccharis sergiloides, Fraxinus trifoli-*

ata, Malosma laurina, Rhus [subgen. *Schmaltzia*] *integrifolia*), do have close relatives in the megafossil record. There also are Miocene and Pliocene pollen records (e.g., Gray, 1960; Martin and Gray, 1962; MacGinitie, 1962, p. 78; Elsik, 1969) of semiwoody genera whose modern species may contribute to coastal sage, notably in *Agave, Ambrosia, Artemisia, Eriogonum, Opuntia, Salvia* and others as well (e.g., "Compositae," "chenopods"). However, these records do not provide definitive evidence as to the existence of coastal sage as a zonal vegetation because they are recorded together with taxa that indicate that the areas in which they lived were sufficiently moist to support forests and woodlands. Further, it is unwise to assume that their mere presence demonstrates, ipso facto, the existence of coastal sage as a zonal vegetation type. As shown earlier for subalpine forest, chaparral, and desert vegetation, this is a doubtful procedure (Axelrod, 1975, 1976, 1977). Finally, these records certainly provide no evidence regarding the origin of coastal sage as a vegetation type.

These mega- and microfossil Neogene records do show that the principal evolution of these taxa had already taken place. Since they occur regularly with taxa representing forest, woodland and dry tropic scrub vegetation, they probably were chiefly border-members of these vegetation zones, favoring localized dry habitats, such as south slopes, sites with thin soil, and those that were especially well-drained (sandy or gravelly). This inference is consistent with two lines of evidence. In the first place, many of the living taxa (e.g., *Artemisia, Encelia, Eriogonum, Baccharis, Malosma, Opuntia, Salvia, Viguiera*) regularly occur in open places today, and notably in those that are disturbed. All of them are "opportunists," for they shift quickly into new open areas, as on stripped steep slopes, road cuts, abandoned clearings, recent burns, and sites opened up by natural earth movements (slumping, sliding). Secondly, the sage taxa that do have megafossil records, and which are essentially inseparable from living species, show that they lived in dry areas where local sites would be suited to them. For instance, *Aesculus palmeri, Fraxinus trifoliata*, and *Malosma laurina* have close allies in the Mint Canyon flora of southern California (age, 12 m.y.). They are associated with species of *Acacia, Bursera, Cardiospermum, Dodonaea, Fouquieria, Lysiloma, Pithecollobium, Rhamnus* and others which indicate that exposed parts of the basin were quite dry and suited to restricted coastal sage communities that probably bordered the live-oak woodland and dry tropic scrub that dominated the basin. In addition, *Rhus integrifolia* has a very similar species in the Tehachapi flora (age, 17 m.y.) where it was associated with desert-border (*Colubrina, Brahea, Conalia, Dodonaea, Euphorbia, Prosopis*) and dry tropic scrub (*Bursera, Ficus, Karwinskia, Leucaena, Sabal*) taxa that indicate a basin of low rainfall in which a rich live-oak woodland dominated. Since the basin was surrounded by a terrain of andesite flows and breccias, these provided very dry sites on south-facing slopes well suited to scattered patches of coastal sage scrub. Another example is provided by the Mt. Eden flora (age, 7 m.y.) of southern California with species similar to *Baccharis sergiloides* and *Malosma laurina*. They lived in a semiarid basin where there were dry tropic scrub and/or desert-border taxa, notably species of *Acacia, Cercidium, Chilopsis, Emplectocladus* (aff. *fremontii*), *Ficus, Forestiera* and *Prosopis*. The basin was bordered by mountains composed of crystalline rocks that contributed coarse detritus to the basin that provided well-drained sites. In addition, low granitic hills within the basin also afforded exposed south-facing slopes suited for coastal sage taxa. Comparable relations are shown by the Anaverde flora (age 10 m.y.) of the western margin of the Mohave area where *Malosma* lived under a semiarid climate. This is inferred from its associates, notably *Colubrina, Eysenhardtia, Dodonaea, Quercus* (scrub oak), *Rhamnus* and *Sapindus*. However, the flora was dominated by oak woodland-grass ("savanna"), with more mesic taxa (palm, *Persea, Platanus, Populus*) along the stream margins.

The fossil records of these woody sage taxa, when coupled with palynological evidence for the occurrence of semiwoody taxa (*Artemisia, Agave, Chenopodiaceae, Compositae, Dudleya*, etc.) in the Neogene (see above), suggest that vegetation allied to coastal sage was confined chiefly to local dry sites under warm, frost-free climate with summer rain. As summer rainfall decreased during the Pliocene, widespread perennial grasslands gradually retreated in California. This was one of the important factors that set the stage for the rise of coastal sage which has supplanted the younger annual grasslands over wide areas. Taxa making up the local patches of Neogene coastal sage in the interior shifted coastward as climate became colder and drier over areas where desert environments now dominate. Since the Neogene taxa living in local sites were already adapted to xeric conditions, they were "preadapted" to spread more widely should dry areas increase in number and area. How and when may this have taken place?

ORIGIN—Several factors have led to the emergence of coastal sage as a zonal (or subzonal) type of vegetation. The major ones include a summer dry climate with an effective rainfall too low for forest or woodland; tectonism that cre-

ated steep slopes too dry for either forest, woodland, or grassland; episodic torrential rainfall that resulted in mass-movement and erosion that stripped slopes and exposed dry areas of bedrock and thin soil suitable for invasion by sage shrubs; and overgrazing, fire, and other activities initiated by man.

Mediterranean climate—The trend to drier climate during the middle and later Tertiary involved a shift in its seasonal distribution, with the elimination of summer rainfall and the gradual emergence of a full-fledged mediterranean-type climate following the Early Quaternary. As drought increased, forests and woodlands retreated and grasslands spread. Shrubs in drier forest and woodland-border sites with a drought-deciduous habit were now at a selective advantage. In the south, taxa with water-storage structures (cacti, *Euphorbia*, *Agave*, *Yucca*) or a drought-deciduous habit (*Aesculus*, *Artemisia*, *Encelia*, *Lycium*, *Rosa*, *Salvia*, *Vigueria*) were also favored as summer drought increased. In addition, a few evergreen shrubs of semiarid to semidesert sites (e.g., *Cneoridium dumosum*, *Malosma laurina*, *Rhus integrifolia*, *Simmondsia chinensis*) were able to adapt, but most retreated to moister sites where they occur in woodland and chaparral.

Coastal sage vegetation thus owes its origin partly to the spread of grassland in semiarid open country as more mesic forests and woodlands retreated. However, coastal sage taxa could not initially invade the spreading grasslands to any major degree because the thick turf and deep soil in areas of low terrain that typified the region were unsuited for shrubs that competed better on well-drained drier and hotter sites with thin soil. These were no doubt present in the lowlands but must have been very restricted in area, as on the bluffs of rivers and especially on south slopes where dry edaphic conditions were present.

Tectonism—At the close of the Pliocene, and continuing through the Quaternary, the mountains of California and Baja California were elevated to their present heights from earlier low hills or positive areas, or from older marine basins. The evidence lies in the folded, faulted and uplifted Early Pleistocene and older sedimentary rocks (see Jahns, 1954, 1973; Christensen, 1966; Gastil, Phillips, and Allison, 1975; Woodburne, 1975). As the Coast Ranges, Transverse Ranges and Peninsular Ranges were elevated, they were rapidly dissected by running water into terrains of diverse relief characterized by deep valleys with steep slopes and thin soil.

At lower, drier elevations, where effective rainfall was less than that which could support forest or woodland, dry slopes and west and south exposures with shallow soil were now suited for shrubs, notably for those of coastal sage vegetation. It is emphasized again that coastal sage is confined to the steepest slopes, and especially to areas where fresh rocks and shallow soil are exposed: sage is not present on steep slopes that are covered with a rich turf of grass and deep soil. Clearly, a major factor accounting for the spread of coastal sage has been the creation of steep slopes, chiefly by tectonism and accompanying erosion. These provided the principal setting for the development of the mosaic of forest-woodland-chaparral-sage vegetation patterns so typical of the region. As the mountains were rapidly elevated they were subject to intense erosion. The coarse detritus (cobbles, boulders, gravel, sand) carried down into the adjacent lowlands was deposited as river terraces and as broad alluvial aprons of relatively low relief. They have provided new, well-drained dry substrates admirably suited for coastal sage taxa, especially in areas of low precipitation, as on the coastal plain south of Colonet, Baja California.

Mass-movement—Episodic flooding by torrential rain, as in the winters of 1934 and 1938 as well as in 1969 and again in 1978—and on innumerable earlier occasions as well—has resulted in major episodes of slumping, mudflows and other mass-movements as well as soil-stripping by sheetfloods (see Troxell and Peterson, 1937; Troxell et al., 1942; Scott and Williams, 1978). These have removed the turf and soil, exposed bedrock (opaline shale, sandstone, granitics, serpentine, gneiss, etc.) and provided a means for the intrusion of dry-adapted shrubs into new dry sites that earlier were largely covered with a thick soil and supported a heavy turf of grass or of forest or woodland vegetation. Coastal sage is more frequent on south- than on north-facing slopes because the former have drier, hotter microclimates which result in a shallower soil and less vegetative cover—both favorable for invasion of sage taxa. In addition, with less vegetative cover, south slopes are more susceptible to mass movements, again favoring the invasion of sage taxa into new open areas. Coastal sage occurs also on other steep slopes, as along fault scarps on the steep rises of river terraces or ocean bluffs. These relations account in part for the spotwise distribution of coastal sage in grassland, woodland and forest areas, for its taxa have invaded newly exposed, open dry sites previously occupied by these vegetation zones. Rapidity of invasion is evident not only from its occurrence in natural fresh exposures, but also in road cuts along new highways. Its persistence

in these dry sites is apparent in old road cuts on State Highway 1 north of Santa Cruz and south of Carmel and on old roads in southern California.

Man—The activities of man have also tended to increase the area of coastal sage. Cattle regularly break the sod during the wet season especially, and in oak woodland-savanna and grassland areas this enables shrubs to invade and become established. Old abandoned fields may revert to coastal sage. Fire also tends to favor sage over grassland, especially on slopes where it clears the turf and semibarren ground becomes exposed after torrential rains. In addition, fire in the lower part of the chaparral belt enables sage shrubs to invade that zone, at least temporarily. In sites where little soil remains, sage may supplant chaparral.

AGE—How old is coastal sage vegetation? Available data suggest that it attained most of its present area since the last glacial, 12,000 years ago. The evidence lies in the nature of Late Pleistocene floras recovered from areas that presently support coastal sage: all of them indicate that rainfall was then sufficient for forest and woodland.

The San Bruno flora, from the east side of the San Francisco Peninsula, occurs in a region that was (prior to urban spread) covered with grassland, oak woodland and patches of Franciscan sage (Potbury, 1932, pl. 2, fig. 2). Dated at 10,000 years B.P. (Berger and Libby, 1966, p. 491), the flora represents a Douglas fir (*Pseudotsuga*) forest (logs 2 meters in diameter) much like that now covering Inverness Ridge 60 km northwest. Rainfall at the lower (drier) edge of the forest in that area (Headquarters, Pt. Reyes National Seashore) averages 810 mm (32 inches) annually as compared with about 460 mm (18 inches) at the fossil site today. Coastal sage taxa, notably *Baccharis pilularis*, *Ceanothus thyrsiflorus*, *Rubus parviflorus*, *Toxicodendron diversilobum*, and *Symphoricarpos albus*, are present in the San Bruno flora but they are also regular members of the *Pseudotsuga* forest. Clearly, if coastal sage was in the area, it must have been highly restricted and confined to the driest, steepest slopes.

A small flora preserved in travertine in old hot spring terraces along State Highway 1 north of the Little Sur River in the Santa Lucia Mountains south of Monterey represents a forest of *Pinus radiata*, *Cupressus* cf. *goveniana* and *Pseudotsuga menziesii* that lived there 10,000 or more years ago (Langenheim and Durham, 1963). Although these authors suggest that the forest was confined to a valley on the steep mountain front, there is no evidence of it in the present terrain; the only valley there is the small gulch that was excavated into the spring-terraces after they were formed. There is reason to believe that forest was more extensive because *Pseudotsuga* indicates considerable rainfall. The area is presently dominated by coastal sage, with species of *Ambrosia*, *Artemisia*, *Baccharis*, *Eriogonum*, *Eriodictyon*, *Diplacus*, *Salvia mellifera* and *Toxicodendron diversilobum* among the commoner shrubs. Several taxa that contributed to the fossil forest, notably species of *Ceanothus*, *Ribes*, and *Rubus*, may have been scattered locally on drier sites and contributed to coastal sage. However, if present, it probably was confined to the driest, rocky, south-facing slopes with an acreage quite limited as compared with its present dominance over the lower slopes of the range here and farther south.

The youthfulness of coastal sage in the coastal strip southwest of Santa Maria is indicated by the occurrence near Pt. Sal of a forest of *Pinus radiata*, *P. masonii* ("*muricata*"), and *P. remorata* (Axelrod, 1967), dated at 28,000 years B.P. (Berger and Libby, 1966, p. 492). The grassland and coastal sage that now cover the slopes of that area have spread more recently. Similar relations are implied by the Carpinteria fossil flora (Chaney and Mason, 1933), which has a revised age of over 40,000 years (personal comm., L. Marcus, Queens College, CUNY, Nos. 467, 468). Climate was sufficiently moist to support *Pinus radiata*, *P. remorata* and *P. masonii* ("*muricata*") on the coastal plain near the shore, and *Pseudotsuga macrocarpa* and *Sequoia sempervirens* lived in sheltered canyons on the slopes of the Santa Ynez Mountains directly north. If coastal sage was present, it must have been confined to the driest, lower slopes of the mountains. In view of the higher precipitation indicated by the fossil flora, coastal sage certainly was more restricted than it is at present in this area where it blankets slopes below the dense evergreen chaparral. Among the shrubs recorded at Carpinteria that may have contributed in a minor way to a restricted coastal sage are *Ceanothus thyrsiflorus*, *Eriodictyon californicum*, *Toxicodendron diversilobum*, and, in local moister sites, *Pteridium aquilinum*. Evergreen shrubs diagnostic of Venturan sage that are not recorded in the Carpinteria flora include *Malosma laurina* and *Rhus integrifolia*, yet they occur in the area today as important elements of coastal sage, implying its more recent spread in the region.

The rich flora from Pit 91 at Rancho La Brea, dated in the range of 40,000 to 25,000 years B.P., and now under investigation by Janet Warter (1976), has species typical of several plant communities. These include closed-cone pine forest, with *Pinus radiata*, *P. masonii* ("*muricata*"),

and *Cupressus macrocarpa*, which indicate a climate too moist for the extensive development of coastal sage over the lowlands of the Los Angeles region. Woodland vegetation is represented by *Juglans californica*, *Juniperus californica*, *Pinus sabiniana*, *Quercus agrifolia*, and *Q. lobata*. Drier slopes supported a chaparral of *Arctostaphylos* (4 or 5 species), *Adenostoma fasciculatum*, *Ceanothus* spp., *Quercus dumosa* and *Rhamnus californica*. Contributing to the riparian woodland that lined stream-courses of the alluvial fan that reached back into the Santa Monica Mountains were *Acer negundo*, *Alnus rhombifolia*, *Cornus californica*, *Platanus racemosa*, *Rubus parviflorus*, *Salix lasiolepis* and *Sambucus mexicana*, as well as diverse aquatic herbs. Noteworthy is the absence from the flora as now known of woody sclerophyll taxa that often dominate the Venturan sage of the area today, notably *Malosma laurina* and *Rhus integrifolia*. This, as well as the absence of their associates, implies that coastal sage was not prominently developed in the area at that time. If present, it must have been confined to the driest slopes on the lower flanks of the Santa Monica Mountains to the north, and was no doubt highly restricted in area.

Diablan sage reaches into the inner slopes of the South Coast Ranges bordering the San Joaquin Valley, where it is composed of many of the taxa of the Lucian sage (Table 2), as well as a number of herbs and some shrubs (e.g., *Haplopappus*: sects. *Ericameria* and *Stenotopsis*) from areas bordering the Mohave Desert (see Sharsmith, 1945). That coastal sage has recently spread in this region is apparent from the San Joaquin flora of Late Pliocene age. It shows that *Quercus douglasioides* (cf. *douglasii*) and *Q. wislizenioides* (cf. *wislizenii*) covered the interfluves. The riparian woodland included abundant *Persea*, *Platanus*, *Populus* and *Umbellularia* that clothed the edge of the seaway there as recently as 4.0 to 3.5 m.y. ago (Axelrod, in prep.). Rainfall in this area must have been near 500–635 mm (20–25 inches) at minimum as compared with 150 mm (6 inches) today. Relief in the nearby area to the west was quite low because the San Joaquin sea trended across the site of the Coast Ranges at this time (Woodring, Stewart, and Richards, 1940). Inasmuch as rainfall increased to the west, as it does today, it seems clear that coastal sage vegetation would have been confined to very local dry sites in the Late Pliocene.

To the south, the McKittrick flora (Mason, 1944), composed of *Pinus monophylla*, *Juniperus californica*, *Arctostaphylos glauca*, *A. pungens*, *Atriplex lentiformis* and *Marah fabaceus*, demonstrates that conifer woodland lived at the edge of the San Joaquin Valley about 38,000 years ago (Berger and Libby, 1966, p. 492). The present area is a desert, with only 125 mm (5 inches) rainfall. As judged from the nearest pinyon pine-juniper community today, situated 48 km (30 miles) south at the south end of Cuyama Valley, the fossil flora indicates rainfall at a minimum was then near 380–500 mm (15–20 inches). Clearly, the area has become much drier in the recent past. This enabled desert vegetation to spread over the lowlands and Diablan sage to cover the drier, steeper slopes where precipitation is greater.

The Early Pleistocene Soboba flora from San Jacinto Valley in interior southern California provides information regarding the history of coastal sage vegetation in that region (Axelrod, 1966). The Soboba flora shows that during an early glacial (Nebraskan?), climate was sufficiently moist to support a mixed forest of *Abies concolor*, *Calocedrus decurrens*, *Pinus ponderosa*, *P. lambertiana*, and *Populus tremuloides* close to or at the floor of the valley, as well as big-cone spruce (*Pseudotsuga macrocarpa*) and Coulter pine (*Pinus coulteri*), and a rich assemblage of woodland and chaparral taxa. The forest could have lived there if precipitation was about 635–760 mm (25–30 inches) at a minimum, whereas rainfall in the area today totals 305 mm (12 inches). Clearly, climate was too moist for Riversidian sage to have formed an important community in this interior region during the Early Quaternary. As the Santa Ana Mountains were elevated and cast a rain shadow over the interior, and as the pluvial period waned, forest retreated fully 1,000 m up into the mountains. To judge from the record of the Late Pleistocene, precipitation was then certainly higher than at present. Hence, coastal sage vegetation would have been more restricted in the Wisconsin than it is today, for the higher rainfall would have enabled oak woodland, grassland and chaparral to dominate over the lowlands. Clearly, the Riversidian sage that dominates the lowlands in the region today is post-glacial in age.

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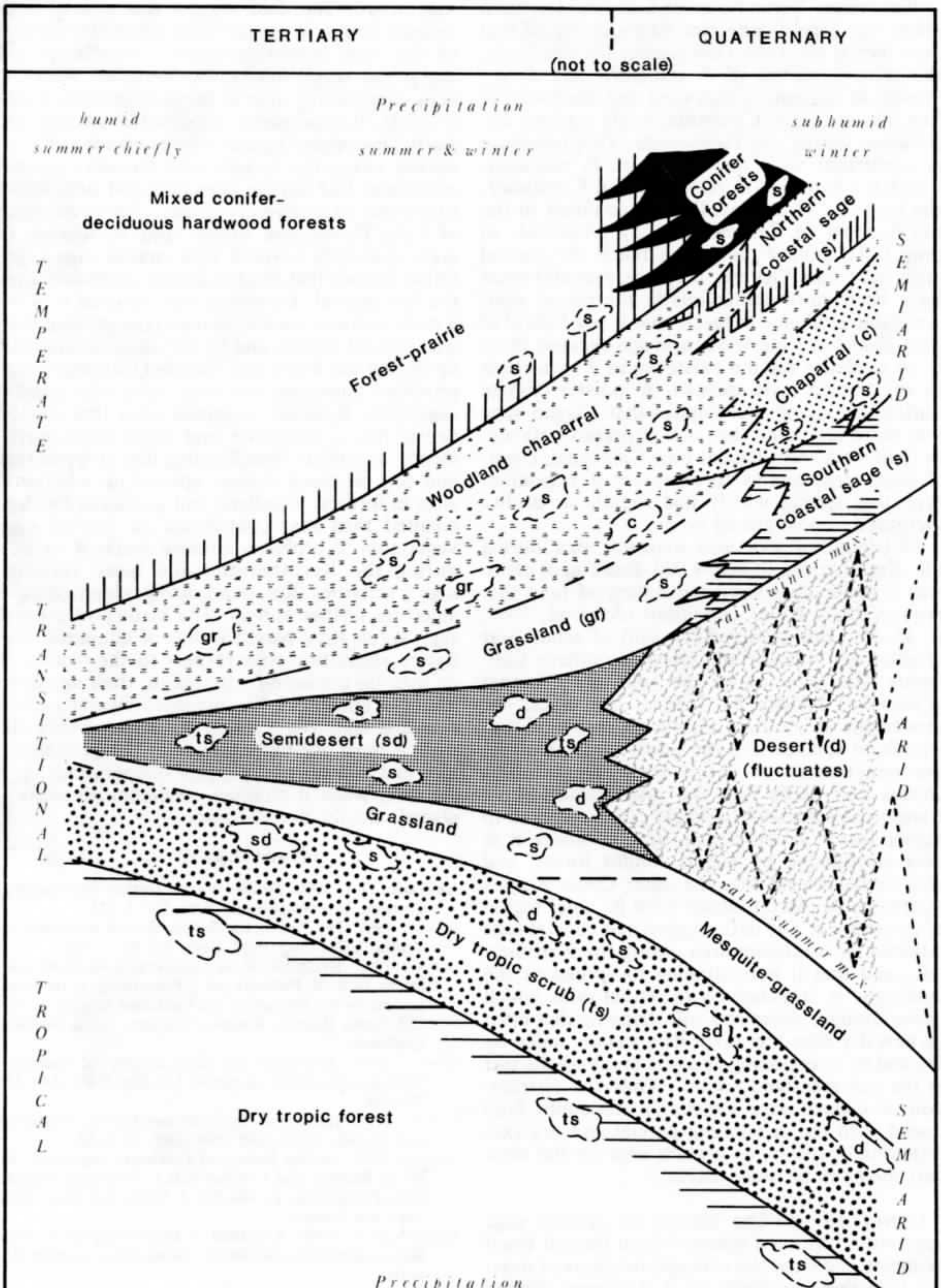
Fig. 3. Suggested historical relations of coastal sage with bordering vegetation zones during the middle and later Cenozoic (not to scale). Localized patches(s) indicate presumed source of coastal sage taxa. As implied by the dashed lines, a major coastal sage adaptive zone was not in existence until after the Early Quaternary. Prior to that, coastal sage was confined to small restricted dry sites adjacent to forest, woodland-chaparral and dry tropic scrub/semidesert vegetation.


TERTIARY
QUATERNARY
(not to scale)
Precipitation
humid
summer chiefly
summer & winter
subhumid
winter
Mixed conifer-deciduous hardwood forests
Conifer forests
Northern coastal sage (s)
TEMPERATE
SEMIARID
Forest-prairie
Woodland chaparral
Chaparral (c)
Southern coastal sage (s)
Grassland (gr)
TRANSITIONAL
Semidesert (sd)
Desert (d) (fluctuates)
rain: winter max.
rain: summer max.
ARID
Grassland
Dry tropic scrub (ts)
Mesquite-grassland
TROPICAL
Dry tropic forest
SEMIARID
Precipitation
summer
summer
summer

Pleistocene floras from the Los Angeles basin show that closed-cone pine forest occupied that area during the Late Pleistocene. On this basis, the present groves of *P. muricata* and *P. remorata* in the coastal hills west and southwest of San Vicente, Baja California, imply a wider distribution during the Pleistocene. This inference is consistent with the nature of *P. muricata* which is a hybrid of *P. remorata* and *P. masonii*, the latter a "living fossil" now confined to the north coast in Sonoma County (Axelrod, in prep.). To have *P. muricata* reach the coastal strip near San Vicente, it (or its parents) must have been more continuous in the recent past. Available evidence suggests that it is a hybrid of post-glacial or Late Wisconsin age because there is no evidence for the existence of *P. muricata* in any known fossil deposit. A moister climate during the last glacial implies that Diegan sage was more restricted than it is at present. Hence, in California and adjacent Baja California, coastal sage scrub seems to represent a vegetation type that spread widely and rapidly as aridity increased in post-glacial time.

Distributional evidence indicates that during the Xerothermic (8,000–4,000 years ago) there was a major coastward movement of taxa that require drier, hotter conditions (Axelrod, 1966, p. 42–55). This involved the shift of semidesert species into interior and coastal southern California; the invasion of the southern Channel (Catalinan) Islands by Diegan sage taxa; the movement of southern California chaparral and woodland species into the south Coast Ranges; the penetration of desert and desert-border shrubs and herbs into the inner south Coast Ranges; and the shift of digger pine woodland to higher levels in the Sierra Nevada where it is now surrounded by mixed conifer forest, and also its movement into the outer Coast Ranges to areas now discontinuous from its chief region of occurrence. The data suggest that coastal sage attained its maximum area during the Xerothermic, and that it is continuing to spread as the landscape is drenched by torrential rains which cause slumps, slides and soil-stripping that open up new dry sites that favor its invasion, aided by fire and by overgrazing as cattle break up the turf in the oak-grassland region. While the distribution of coastal sage vegetation no doubt fluctuated with the alternating pluvial and dry (xerothermic) periods, its present area for the most part seems to be quite recent.

CONCLUSIONS—The history of coastal sage vegetation has been inferred from limited fossil evidence and from the ecologic relations of modern taxa that contribute to it. Neogene climate was too moist for a widespread (zonal) coastal sage scrub. The data suggest that coastal sage species similar to modern taxa inhabited restricted dry sites bordering forests, woodlands and dry tropic scrub during the Neogene, with the taxa contributing also to these vegetation zones (Fig. 3). It was highly localized even into the Early Quaternary because the lowlands still supported extensive forests and woodlands, and mountains had not yet been elevated sufficiently to provide extensive dry slopes. The occurrence of Late Pleistocene forests and woodlands in areas presently covered with coastal sage vegetation implies that its area greatly increased after the last pluvial. Its spread was favored now by a more extreme mediterranean-type climate than was present earlier, and by the steep terrain built up during the Early and Middle Quaternary that provided numerous dry sites suited for coastal sage taxa. Episodic torrential rains that caused debris flows, mudflows and other mass-movements, as well as sheetflooding that stripped turf and soil on steep slopes, opened up additional sites in forests, woodland and grassland for dry-adapted taxa that contributed to coastal sage vegetation. It probably attained much of its area during the Xerothermic, and more recently man's activities (fire, overgrazing, clearing) have aided its further spread. The history of coastal sage scrub thus parallels that of chaparral and desert vegetation with respect to the source of its taxa (in bordering vegetation), their age (pre-Miocene and later), the increased diversity of its taxa and adaptive types in the region where climate is most like that of the later Neogene (summer and winter rain, equable temperature), and the time when it attained maximum area (post-glacial, chiefly Xerothermic).

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